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SYSTEMATIC NOTES ON THE LOONS (GAVIIDAE: AVES)

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ABSTRACT. The following discussion documents the treatment of the loons for the revision of Volume 1 of Peters' *Check-list of Birds of the World*. The family is thought to be most closely related to the Charadriiformes. The Cretaceous genera *Enaliornis* and *Lonchodytes* are thought to be convergent with rather than related to the loons (*contra* Brodkorb). *Gavia immer* and *G. adamsii* are considered full species but members of the same superspecies, while *pacifica* is considered conspecific with *arctica*. The subspecies *Gavia stellata squamata*, *G. arctica suschkini*, and *G. immer elasson* are not recognized. The sequence of forms followed is: *stellata*, *arctica pacifica*, *a. arctica*, *a. viridigularis*, *immer*, *adamsii*.

I. INTRODUCTION

The purposes of this paper are to present reasons for decisions made in preparing the section on the Gaviidae for the revision of Volume 1 of Peters' *Check-list of Birds of the World* and to present some preliminary information gained while examining and measuring specimens of loons preparatory to making an analysis of geographic variation within the family. To date, I have examined over 2200 study skins of loons but still need to study material in several important collections before the final analysis can be made.

For a group of only four species, there have been many divergences of opinion on such matters as the systematic position of the family, the sequence of species within the genus, the specific status of some of the forms, and the validity of several of the subspecies.

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II. SYSTEMATIC POSITION OF THE LOONS

There is general agreement that the living loons belong to the single genus *Gavia*. This, with one or two genera known only as fossils, constitutes the family Gaviidae. Several fossil genera referred to families of uncertain systematic position have also been included in the order Gaviiformes, which otherwise contains only the Gaviidae. These fossils are discussed below.

The varied opinions on the systematic position of the living loons within the class Aves have been well summarized by Sibley and Ahlquist (1972: 53-58). On the basis of fossil evidence (Storer, 1956) and studies of egg-white proteins (Sibley and Ahlquist, *loc. cit.*), loons are believed most closely related to the gulls, auks, and shorebirds. Ideally, they should be placed next to or near the Charadriiformes, but this is impractical as only the first volume of Peters' check-list is being revised at present.

III. SEQUENCE OF SPECIES

In presenting a linear sequence of species, it is customary to start with the most primitive and end with the most advanced. In the case of the loons, there is fossil evidence bearing on the matter of primitiveness.

The known fossil record of these foot-propelled diving birds goes back to the Upper Eocene of England (*Colymboides anglicus*) and the Aquitanian deposits (late Oligocene or early Miocene) of France (*C. minutus*) and probably the Oligocene of North America (*Gaviella pusilla*). The Lower Cretaceous genus *Enaliornis* and the Upper Cretaceous genus *Lonchodytes* have been considered as families of the same order (Gaviiformes) as the loons by Brodkorb (1963a: 220-221; 1963b: 56-60). However, the material of these genera is fragmentary, and the pieces of leg bones resemble those of loons in showing adaptations for swimming and diving but in other respects are quite different from them. The distal end of the carpometacarpus of *Lonchodytes pterygius*, as shown in Brodkorb's figure (1963b: 59), differs so markedly in the relative sizes, angles, and positions of the distal articulations from those of the loons as to cast considerable doubt in my mind on the alleged phylogenetic relationship between *Lonchodytes* and *Gavia*.

If, as I am convinced, these Cretaceous genera are convergent with the loons and if we accept Brodkorb's comment that the position of the little-known Upper Paleocene genus *Eupterornis* is "tentative," the earliest known loons (*Colymboides* and *Gaviella*) were smaller than later ones. The best-known species (*C. minutus*) was about the size of a teal, and, judging from the size of its wings, a strong flier (Storer, 1956: 423). The earlier species (*C. anglicus*) is poorly known but was somewhat larger and apparently had relatively shorter wings than *C. minutus*. It may have "represented a specialised offshoot from a more generalised gaviid stem, rather than a direct ancestral form of either the later *Gavia* species or *C. minutus*" (Harrison, 1976: 66). The Oligocene species, *Gaviella pusilla*, was also smaller than the species of *Gavia*. Known only from the proximal end of a carpometacarpus, *Gaviella* differs from other loons in several respects and is probably not closely related to them (Wetmore, 1940: 30). Thus the limited evidence from fossils indicates that *Gavia* evolved from smaller birds which were less well adapted for diving and had relatively larger wings. While the modern genus *Gavia* contains several Pliocene species, studies of these species have not as yet provided information regarding the relative antiquity or phylogenetic relationships among the Recent species.

The Red-throated Loon, *Gavia stellata*, is the most distinct species in both its winter and nuptial plumages, and for this reason it should be placed at one end of the sequence. The square white spots on the upperparts and the well-developed stripes and iridescence on the head and neck of the other three species can be considered advanced characters. *G. stellata* is the smallest of the living loons and also has the lowest wing loading. To estimate this, I divided the weight of the bird by the square of the length (arc) of the folded wing. The means of this index for ten specimens of each of the species are as follows: *stellata* 2.00, *a. pacifica* 2.25, *immer* 3.03, and *adamsii* 3.17 grams/cm². Although detailed comparative studies have not been made, *stellata* is said to be able to take off from water more easily than the other loons and alone among them can take off from land (Palmer, 1962: 59). As pointed out above, small size and greater flying ability may be considered primitive characters in loons, so I have placed *stellata* first on the basis of its relatively simple nuptial plumage, small size and good flying ability.

As members of a superspecies, *adamsii* and *immer* should be placed next to each other. *Arctica* has been known to hybridize with *immer* (Hunter and Dennis, 1972; Robertson and Fraker, 1974) and therefore these two species should be adjacent on the list. Assuming the largest species to be the most advanced and lacking other strong evidence to the contrary, I prefer the sequence *arctica*, *immer*, *adamsii* to the reverse for these three species. If one considers the forms of *arctica* to represent a broken rassenkreis, as I do, the sequence should be either *pacifica*, *arctica*, *viridigularis* or the reverse. I prefer starting with the smaller, better-known form, and thus the sequence I have adopted is: *stellata*, *arctica pacifica*, *a. arctica*, *a. viridigularis*, *immer*, *adamsii*.

IV. SPECIES PROBLEMS

THE COMMON AND YELLOW-BILLED LOONS, *G. immer* and *G. adamsii*. — The breeding ranges of these forms were presumably separated during the last glaciation — that of *immer* lying south of the glaciers and that of *adamsii* in Yukon-Bering Sea refugia to the north (Rand, 1948: 317–318). Of the principal differences between the species, the color of the bill and of the iridescence on the head and the head patterns may have been selected for as reproductive isolating mechanisms; all are located where major specific differences among other groups of diving birds such as penguins and grebes are found. On the other hand, evolution in bill shape in *adamsii* was presumably related to feeding. The upturned mandibles of this species and of *stellata* appear to be adaptations for bottom foraging. When birds are moving close over the bottom, the bill must be held below the body to catch bottom-living prey. In this position of the head, the lower part of the upturned mandible would lie nearly parallel to the bottom, making capture of prey in this situation easier than if the bill were shaped like those of *immer* and *arctica*. The upturned bills of *adamsii* and *stellata* are probably an example of convergence, because there is no other reason to consider the former more like *stellata* than it is like either of the other two species. The difference in size between *immer* and *adamsii* might be accounted for by Bergman's rule, and like bill form, is probably not primarily related to reproductive isolating mechanisms.

The effectiveness of the isolating mechanisms mentioned above is evident in the paucity or lack of known hybrids between the two

species. There is an adult "female" in the Royal Ontario Museum (No. 76,360) found dead at Pt. Credit, Ontario on December 7, 1957, which has been thought to be a hybrid between *immer* and *adamsii* (Godfrey, 1966: 11). In the recurved lower outline of the proximal segment of the mandibular rami (character 6 of Binford and Remsen, 1974: 115) this specimen resembles *adamsii*. The size of the remaining white squares on the back are within the range of those of *adamsii* and of males of *immer*, but not of females of *immer*. In size of wing, tarsus, and bill, the bird is well within the range of males of *immer*. In the other bill characters described by Binford and Remsen, the specimen is within the range of *immer*. While the possibility that this bird is an *immer* — *adamsii* hybrid cannot be completely discounted, I think it is more probably a male *immer* which was mis-sexed by the collector, who recorded nothing concerning the size or condition of the gonads.

THE STATUS OF *pacifica*. — The three forms of the Arctic or Black-throated Loon (*arctica*) complex (*arctica*, *viridigularis*, and *pacifica*) replace one another around the arctic except in Iceland and Greenland, where none occurs. Thus they might be thought of as forming a broken rassenkreis. The nominate form, *arctica*, ranges from the British Isles eastward across the northern parts of Eurasia and intergrades with *viridigularis* in Siberia. The latter form is found in western Siberia, largely south of the range of *pacifica*, and in parts of western Alaska. The widespread North American form, *pacifica*, also breeds in northeastern Siberia. Portenko (1939) and Bailey (1948) have shown that the breeding ranges of *pacifica* and *viridigularis* overlap in Anadyrland and western Alaska and reported no interbreeding. They concluded that the two were, therefore distinct species, an opinion followed by Vaurie (1965).

There are several reasons for doubting the specific status of *pacifica*. In the first place, those who have discussed the problem in the past have ignored one pertinent question: would *arctica* and *pacifica* interbreed if their ranges were to expand and meet? I think it likely that they would because the throat color is the same and the difference in size is less than that between *pacifica* and *viridigularis*. Secondly, there has been no thorough, detailed field study of *pacifica* and *viridigularis* in the area of overlap, and thirdly, there is evidence of interbreeding between the two forms.

Of the two forms, *viridigularis* is larger in all measurements, has a green (not purple) sheen on the throat, and a darker gray nape.

Green- or blue-throated individuals, otherwise indistinguishable from typically purple-throated individuals of *pacifica* are known to occur (Bailey, 1948: 140; Palmer, 1962: 45; Vaurie, 1965: 5), but whether this is a result of introgression with *viridigularis* or part of the normal range of variation of *pacifica* is unclear. To date, I have measured and examined 12 examples of *viridigularis* and approximately 270 of *pacifica* in breeding plumage. Of the latter, at least nine, or 3.3 percent have green or blue-green throats. All nine have measurements well within the range of *pacifica*. In addition, a male from Savoonga, St. Lawrence Island, Alaska (Colo. Mus. Nat. Hist. No. 26,769) labelled "*viridigularis*" has measurements well within the range of *pacifica*, although all above the means for males of that form. The nape is dark, like that of *viridigularis*, and it is either a very small example of that form or an intergrade. Two other green-throated birds may be intergrades: a male (Nat. Mus. Canada No. 8,816) from Barter Island, Alaska, has a nape intermediate in color between those of the two forms, a long wing (318 mm. or nearly 1.5 standard deviations above the mean for *pacifica*), a long tarsus (near the maximum for *pacifica*), but a small bill (below the mean for males of *pacifica*); and an unsexed bird (Amer. Mus. Nat. Hist. No. 348,959) from SE Victoria Island, Canada, has a light nape, long wing (321 mm.), a short tarsus (between the means for males and females of *pacifica*), a long bill (above the mean for males of *pacifica*) and a deeper bill than that of any *pacifica* I have measured. Two purple-throated males with long wings (323 and 325 mm.), long tarsi, and bills somewhat above the mean for males of *pacifica*, are also within the range of *viridigularis* in all these measurements and may be intergrades. While the sample of *viridigularis* which I have seen to date is too small to permit an accurate analysis of variation within that form, the presence of several probable intergrades suggests that interbreeding occurs between it and *pacifica*.

V. SUBSPECIES PROBLEMS

Gavia stellata squamata Portenko. — Vaurie (1965: 4) lists this subspecies as not well differentiated but warranting nomenclatural recognition, while Dement'ev and Gladkov (1968: 291) question its validity. I have examined 12 breeding adults from the range of this form from Franz Josef Land (3), Spitsbergen (7), and Bear Island (2), and I find that the plumage characters used to

differentiate this form from nominate *stellata* (Vaurie, *loc. cit.*) are not consistent within the population, and as Dement'ev and Gladkov (*loc. cit.*) pointed out, are found in some specimens from outside the range. On the evidence now available, I see no value in recognizing this subspecies.

Gavia arctica suschkini Zarudny. — Although this race, based on migrant individuals from Russian Turkestan, was recognized by Peters (1931: 34), it is generally considered a synonym of the nominate race by recent authors (e.g. Dement'ev and Gladkov, 1968: 297; Vaurie, 1965: 5). I have not seen the material on which this race was based and follow the above authors in not recognizing *suschkini*.

Gavia immer elasson Bishop. — This subspecies was also recognized by Peters (1931: 35), but not by Vaurie (1965: 7) and many other recent authors. This species varies greatly in size, wing lengths of adults ranging at least from 287 to 411 mm., but I have not collected sufficient data to work out the pattern of geographic variation, which appears to be largely clinal. While realizing the possibility that there may be recognizable subspecies within this species, I prefer to consider *immer* monotypic at least until a thorough revision can be made.

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